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ON SOME POINTS IN THE PHYLOGENY OF THE PRIMATES.

BY ARTHUR ERWIN BROWN.

The suggestions here offered, as to the possible origin of certain structural resemblances noted between anthropomorpha and one of the family groups of existing lemurs, have resulted as a by-product from a study of the interrelations of the *Primates*, undertaken with a different purpose; they are put forth simply as a contribution to the sum total of possibilities which, upon final sifting, shall some day determine the exact degree and manner of the relationship between men, apes and monkeys, and not in any sense as a demonstrated conclusion—for the reaching of which more detailed knowledge of the early Tertiary mammals is required.

In accounting for the later stages in the phylogeny of man, three hypotheses are to be considered.

The view of Darwin,¹ now held by a majority of systematists, is that the anthropomorpha (here used to include man and the higher apes) branched off from the main stem of monkeys after its divergence from the lemurs.

In 1860, Gratiolet² was led by a study of brain characters alone, to the conclusion that each genus of anthropoid apes was descended from an existing genus of monkeys; thus he derived *Gorilla* from *Cynocephalus*; *Anthropopithecus* from *Macacus*; *Simia* and *Hylobates* from *Semnopithecus*. This view has received little support and the facts now known show its complete untenability.

Lastly, Prof. E. D. Cope³ has suggested a common origin for the anthropomorpha directly from the Eocene lemuroids, independently of the line by which the monkeys came from the same stock, being led to this conclusion by a study of the tendency in certain races of men to the production of tritubercular upper molars, which tendency he interprets as reversion, or retrogressive

¹ *Descent of Man*, Chapter VI.

² *Comptes Rendus*, 1860, p. 801.

³ *Journal of Morphology*, 1888, p. 21, and *Primary Factors of Organic Evolution*, p. 154 (1896).

evolution toward an ancestral lemuroid tritubercular dentition. It appears to me that this observation of Cope's does not stand alone, and my present purpose is to indicate certain homologies which appear to fall into line with it.

In estimating the degree of relationship between men and apes, on the one hand, and catarrhine monkeys on the other, and that borne by each series to their ancestral group, two sets of homologies are of especial value—those which the anthropomorpha share with some, at least, among lemurs (in which catarrhine monkeys have no part), and those connecting catarrhines with lemurs, which are, conversely, absent from anthropomorpha.

Some correspondences of much weight are disclosed by the teeth and the vertebral column; these will be briefly recapitulated without extended description of details, which have already been given in each case by recognized authorities, although it does not appear that due weight has been given to their bearing upon the present question. It may be added that almost all have been verified by my own observations.

In anthropomorpha there is an oblique ridge crossing the crowns of the upper molars from *protocone* to *metacone*.⁴ This is present with great uniformity in the first and second human molars, as well as in the third when it presents the quadritubercular form, and in examination of a considerable number of skulls belonging to all four genera of anthropoids, I have found it in every case where the crowns were sufficiently unworn to permit its disclosure. Topinard lays much stress upon this crest and expresses the opinion that it represents the posterior border of the primitive three-cusped tooth,⁵ from which the four-cusped has been evolved by addition of a postero-internal cusp (*hypocone*). He states, further,⁶ that the crest is never absent in platyrhine monkeys—an assertion which appears to me too sweeping, but traces of it are certainly found in *Ateles* and *Alouatta*, and perhaps irregularly in other genera. It is not found in any catarrhine monkey, but reappears in the quadritubercular lemurs of the family *Nycticebidae*,⁷ comprising

⁴ Owen, *Odontography*, Pl. 116, fig. 6, and *Comp. Anat.*, III, p. 320; Huxley, *Anat. Vert.*, pp. 390, 396, 412 (direction of ridge reversed), and *Proc. Zool. Soc. of London*, 1864, p. 314 *et seq.*; Mivart, *P. Z. S.*, 1864, p. 611 *et seq.*; Topinard, *L'Anthropologie*, 1892, p. 641 *et seq.*

⁵ *l. c.*, p. 650.

⁶ *l. c.*, p. 683.

⁷ Huxley, *l. c.*, pp. 322-324; Mivart, *l. c.*, p. 631; Topinard, *l. c.*, p. 691.

Loris, *Nycticebus*, *Perodicticus* and *Arctocebus*, and irregularly in *Microcebus*⁸ and *Galago*.⁹ Of especial significance is the fact that some of the more recently described Eocene *Primates*¹⁰ present both a small fourth cusp and traces of the oblique ridge on the first and second upper molars. In all catarrhine monkeys both upper and lower molars are quadricuspid, with strong transverse ridges connecting the opposite cusps.¹¹ This arrangement is not found in anthropomorpha, but is shown both above and below in *Indris*,¹² while *Loris* and *Arctocebus* show it in the lower jaw.

Mr. Mivart¹³ directs attention to the fact that in man the spinous process of the third cervical vertebra is short and bifurcated; in anthropoids it is elongated and simple, while in monkeys generally it is short and simple, as is the case in lemurs excepting in the *Nycticebidae*, among which in *Nycticebus* it is quite human, while in *Perodicticus* and *Arctocebus* it is anthropoid. Similar correspondences are exhibited by other parts of the spinal column. In anthropomorpha the spinous processes of the lumbar and the last, or last two, dorsal vertebrae are directed backward, the transverse processes are turned slightly backward (dorsally), and the anapophyses and metapophyses are few in number and feebly developed. In catarrhine monkeys the corresponding spinous processes are bent forward, so as to make a distinct point of convergence about the next to the last dorsal with those of the anterior vertebrae, which are inclined strongly in the opposite direction; the transverse processes are horizontal or more usually slightly bent forward (ventrally), and the anapophyses and metapophyses are strongly developed and begin usually in advance of the seventh dorsal, extending posteriorly through the whole of the lumbar vertebrae.

In all these respects lemurs agree with monkeys, excepting again the *Nycticebidae*, where the disposition is generally as in anthropomorpha.

⁸ Mivart, *l. c.*, p. 621.

⁹ Huxley, *l. c.*, p. 325, fig. 5; Mivart, *l. c.*, p. 625; Topinard, *l. c.*, p. 692.

¹⁰ H. F. Osborn, *Bull. Am. Mus. of Nat. Hist.*, 1895, p. 19, fig. 4, and *International Dental Journal*, July, 1895, Pl. AA, fig. 10.

¹¹ Huxley, *Anat. Vert.*, p. 401; Topinard, *l. c.*, p. 679.

¹² Huxley, *P. Z. S.*, 1864, p. 326; Topinard, *l. c.*, fig. 8, T.

¹³ *P. Z. S.*, 1865, p. 550.

¹⁴ Mivart, *P. Z. S.*, 1865, p. 545 *et seq.*

The sacrum in anthropomorpha is composed of five or six coalesced vertebrae; in monkeys the normal number is two or three, and a like number is shown by lemurs, except *Indris*, which has four, and *Perodicticus* and *Arctocebus*, each of which has five.¹⁵

Now if we attempt, from Gratiolet's standpoint, to account for the presence in anthropoids of so many of the above characters as their supposed ancestors do not possess, inheritance being excluded by the very terms of the hypothesis, we are driven to analogous variation as the only process with which we have any acquaintance which might be held competent to explain them.

But, so far from there being any good reason to assume that analogous variation has been a frequent method in nature, there is, on the contrary, warrant for an *à priori* belief that the mere mathematical chances against the occurrence of any single case of it are very great; so that where, as in the present circumstances, seven cases of the independent development of almost exactly similar characters must have taken place in each of four genera (to say nothing of man, who is not provided for by the hypothesis), the improbability becomes so enormous as to remove it from rational consideration.¹⁶

The theories of Darwin and of Cope remain to be examined, and it may be said at once that no one of the homologies which have been noted is excluded by either of them, but there is, in my belief, a wide difference in their relative probability; that of Cope being so far the most simple, that it is logically indicated for our acceptance.

Darwin's hypothesis requires us either to suppose that there has been an extensive and complicated process of preservation of certain structures and suppression of others, in which the family groups now differ, or to take refuge again in analogous variation. Both are rendered difficult of acceptance by the reflection that of the characters here advanced few, if any, can be believed to have been adaptive. It is unsafe to dogmatically assert that a given structure

¹⁵ Mivart, *P. Z. S.*, 1865, p. 560.

¹⁶ Furthermore, the same principle must be invoked to account for the absence of the cusp-bearing heel on m_3 , possessed by each of the supposed ancestral genera; for the presence of three external cusps on the lower molars; the presence of a vermiform appendix; the independent origin of the left common carotid from the arch of the aorta, and the converging direction of the hair on the arms toward the elbow, all of which are peculiar to anthropomorpha.

can never have been of adaptive character, but we are at least entitled to consider that if monkeys in general have flourished luxuriantly with transverse ridges on the crowns of their upper molars, and at most three sacral vertebræ, a slight oblique ridge on the upper teeth and two or three additional vertebræ in the sacrum can hardly be supposed to have had selective value to anthropoids.

The remaining theory, that of Cope, would account for the conditions noted by the process of direct and simple inheritance, and requires no greater amount of assumption than has more than once been justified in the course of phylogenetic speculation. Fragmentary as are the remains of the Eocene lemuroids which have come to light, they are enough to show that while the group as a whole was generalized, it yet presented at that early period, a considerable amount of variety in details, many of which have been preserved in existing lemurs. Of these early forms we have remains of little but jaws and teeth, but the many and curious correspondences which have been noted between anthropomorpha and the *Nycticebidae* are best intelligible upon the supposition that they originated in a group which, possessing the tooth characters shown by each, had associated with them the other structures as well; such may have existed among the *Anaptomorphidae*, but in the present state of ignorance as regards the details of the remaining skeletal structure of that group, it would be rash to attempt a close specification, either of the particular form or of its geographical region.

Cope's view of the independent origin of the anthropomorpha was based upon the supposed tendency in the human race to revert to a tritubercular form of molar. There are minds to which reversion is but a convenient term denoting a process which it is rarely possible to either prove or disprove; but whether or not it be accepted in this case,¹⁷ Prof. Osborn has figured the upper jaw of a *Primate*¹⁸ (possibly *Indrodon*) from the Puerco beds, possessing quadratubercular upper molars, with traces of an oblique ridge—an observation which greatly fortifies Cope's position. His case of reversion, if admitted, would then lead a stage further back to

¹⁷ It is to be observed that Topinard's refutation (*l. c.*, p. 707) of Cope's hypothesis is based upon a misunderstanding of its real terms.

¹⁸ *Bull. Am. Mus. of Nat. Hist.*, 1895, p. 19, fig. 4.

the primitive three-cusped molar, which was in all certainty that typical of the earliest lemuroids.

The better agreement of this hypothesis with the successional relations shown by palaeontology, must be emphasized, for as far as can now be determined, apes of anthropoid character, such as *Pliopithecus* and *Dryopithecus*, were already differentiated in the middle Miocene, at which time, or even later, monkeys appear to have been represented only by such intermediate forms as *Mesopithecus*. No existing genus of catarrhine monkeys is known from earlier deposits than *Papio* and *Macacus* from the Sivalik beds of lower Pliocene age, in which deposits other remains have been found which there is reason to regard as referable to *Anthropopithecus* and *Simia*. The fact that before monkeys as now known, began to exist, man-like apes were far advanced in development, and that the earliest evidence of existing genera of apes is coeval with that of existing genera of catarrhines, tells enormously in favor of the early and independent origin of anthropomorpha.

The objections to this view which arise from the closer correspondence of anthropomorpha with monkeys, rather than with lemurs, in many soft parts of the organism, are not to be overlooked; but the remarkable differences in placentation and in the anatomy of the sexual organs disclosed by closely related genera, and even species, in other groups; the smooth brains of marmosets among monkeys, and the readily adaptable character of muscular dispositions, and all structures relating to locomotion, renders these characters of more or less uncertain value in classification.

It is no part of the present purpose to inquire closely into the corresponding stages in the pedigree of the remaining *Primates*, to do which, indeed, we are yet too ignorant of many essential details, but this much may be said: the *Nycticebidae*, which suggest so many human and simian traits, are far from being typical lemurs, with which in general structure the monkeys show much agreement; but catarrhines and platyrhines are wide enough apart in many ways, and the period during which they have been thus separated is so immeasurable, as to suggest the greater probability that their chief characteristics were already differentiated in their respective Tertiary forerunners. The remarkable fact that some platyrhine genera, as *Ateles*, present traces of nearly all the modifications which have been noted as characteristic of anthropomorpha

and the *Nycticebidæ*, perhaps supports this view, but at the same time well illustrates the complexity of the problem.

If the progress of palæontology should justify these speculations, it seems to follow that it is likely to also demonstrate the multiple rather than the single origin of the present *Lemuroidea*.